# Skeletal muscle adaptations during early phase of heavy-resistance training in men and women

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Staron, R. S., D. L. Karapondo, W. J. Kraemer, A. C. Fry, S. E. Gordon, J. E. Falkel, F. C. Hagerman, and R. S. Hikida. Skeletal muscle adaptations during early phase of heavy-resistance training in men and women. J. Appl. Physiol. 76(3): 1247-1255, 1994.—An 8-wk progressive resistance training program for the lower extremity was performed twice a week to investigate the time course for skeletal muscle adaptations in men and women. Maximal dynamic strength was tested biweekly. Muscle biopsies were extracted at the beginning and every 2 wk of the study from resistance-trained and from nontrained (control) subjects. The muscle samples were analyzed for fiber type composition, cross-sectional area, and myosin heavy chain content. In addition, fasting blood samples were measured for resting serum levels of testosterone, coristol, and growth hormone. With the exception of the leg press for women (after 2 wk of training) and leg extension for men (after 6 wk of training), absolute and relative maximal dynamic strength was significantly increased after 4 wk of training for all three exercises (squat, leg press, and leg extension) in both sexes. Resistance training also caused a significant decrease in the percentage of type IIb fibers after 2 wk in women and 4 wk in men, an increase in the resting levels of serum testosterone after 4 wk in men, and a decrease in cortisol after 6 wk in men. No significant changes occurred over time for any of the other measured parameters for either sex. These data suggest that skeletal muscle adaptations that may contribute to strength gains of the lower extremity are similar for men and women during the early phase of resistance training and, with the exception of changes in the fast fiber type composition, that they occur gradually.

fiber types; myosin heavy chains; hypertrophy; resistance training

TWO MAJOR FACTORS, neural adaptations and hypertrophy, contribute to stength gains. Neural factors involve adjustments within the nervous system for the acquisition of a skill and maximal activation of the muscle (more efficient recruitment, increased neural activation, motor unit synchronization, and excitability of the  $\alpha$ motor neurons and/or motor end plates and decreased Golgi tendon organ inhibition) (see Refs. 9, 16, 24). Hypertrophy of skeletal muscle involves an increase in the cross-sectional area of individual muscle fibers and possibly (although to a lesser extent) hyperplasia (2, 34).

Although various studies have demonstrated the important role played by the nervous system in strength gains during the early phase (initial 6–8 wk) of resistance training in untrained individuals (24), recent evidence from our laboratory suggests that intramuscular adjustments also take place during this time (31, 32). Indeed, significant hypertrophy of all major muscle fiber types (I, IIa, and IIb) and fast fiber type conversions (type IIb  $\rightarrow$ 

IIa) have been found in the vastus lateralis muscle of women after just 6 wk of high-intensity resistance training (32).

Using a series of successive biopsies taken before and every 2 wk during 8 wk of heavy-resistance training, this study was designed to 1) examine the time course for specific muscular adaptations (cross-sectional area changes and fast fiber type conversions) during the early phase of resistance training and 2) investigate possible adaptational differences between previously untrained men and women.

## MATERIALS AND METHODS

Subjects. Thirty-five healthy individuals (21 men and 14 women) volunteered to participate in the present investigation. All subjects signed informed consent documents, and approval was given by the Ohio University Institutional Review Board before the beginning of the study. Two subjects (1 man and 1 woman) dropped out after the initial biopsy. Therefore, a total of 33 individuals completed the study. The resistance training group consisted of 13 men (age  $23.5 \pm 3.2$  yr, height  $1.77 \pm 0.08$  m) and 8 women (age  $20.6 \pm 1.5$  yr, height  $1.66 \pm 0.05$  m). The training subjects had not previously been involved in any heavy-resistance training. Of the remaining 12 individuals, 7 men (age  $20.7 \pm 1.4$  yr, height  $1.80 \pm 0.09$  m) and 5 women (age  $20.6 \pm 1.6$  yr, height  $1.61 \pm 0.01$  m) were physically active but were not involved in any resistance training or regular exercise; these subjects served as controls.

Anthropometric measurements. Body composition and thigh girth were determined at the beginning (week 1) and every 2 wk during the 8-wk high-intensity training (weeks 3, 5, 7, and 9). Body composition was estimated using skinfold measurements from three sites (anterior thigh, posterior brachium, and suprailium) (13). Circumference measurements were taken from the relaxed right lower limb at three sites: 1) 5 cm above the superior aspect of the patella, 2) immediately inferior to the gluteal fold, and 3) midway between these two sites.

Training protocol. The training protocol was similar to that in our previous resistance training studies (31, 32). Briefly, the training period consisted of a 1-wk preconditioning-orientation phase (week 1) followed by 8 wk of high-intensity resistance training (weeks 2-9). Three lower limb exercises for the quadriceps femoris muscle group (squat, leg press, and leg extension) were performed twice a week (Monday and Friday) with every other Wednesday used for maximal dynamic strength [1 repetition maximum (1 RM)] testing. Workouts consisted of two warm-up sets followed by three sets to failure of either 6-8 repetitions (Mondays) or 10-12 repetitions (Fridays) for each of the three exercises with  $\sim 2$  min of rest between sets. The weights were progressively increased to maintain this range of repetitions per set. Workouts began and ended with 10-15 min of flexibility exercises combined with calisthenics.

Serum collection. After the subjects had fasted for 12 h, 10-15 ml of blood were drawn from the median cubital vein with use

of a needle, syringe, and vacutainer assembly with the subjects in a slightly reclined seated position. Blood samples were taken before the initial biopsy and every 2 wk (on Friday mornings) during the high-intensity training (24 h before each muscle biopsy). The subjects abstained from ingesting any substances containing alcohol or caffeine during the fasting period and did not perform strenuous exercise for at least 36 h before giving blood. Identical blood collection procedures were used throughout the study. Blood samples were taken at the same time of day to reduce the effects of diurnal variations on hormonal concentrations. The subjects reported to the laboratory and sat quietly for 10-15 min before giving a blood sample. Whole blood was allowed to clot at room temperature and was centrifuged at 1.060 g for 10 min. Subsequently, 4-5 ml of serum were removed and stored in 1-ml aliquots at  $-70^{\circ}$ C until analysis was performed.

Hormone analyses. The subjects were nonsmokers, had no history of any endocrine disorders or drug use (including androgenic-anabolic steroids), and were not on any medications or nutritional supplementation during the course of the investigation. Resting serum testosterone and cortisol concentrations were determined in duplicate using single-antibody solidphase <sup>125</sup>I radioimmunoassays (Diagnostic Systems Laboratories, Webster, TX). Intra- and interassay variances were 4.5 and 5.2% for testosterone and 3.1 and 4.8% for cortisol, respectively. Resting serum growth hormone concentrations were determined in duplicate using a double-antibody liquid-phase <sup>125</sup>I radioimmunoassay (Diagnostic Systems Laboratories). Immunoreactivity was measured with an LKB 1272 Clinigamma automatic gamma counter with an on-line data reduction system (Pharmacia LKB Nuclear, Turku, Finland). Samples were thawed only once and were decoded after all analyses were completed (blinded procedure).

Muscle biopsies. Muscle biopsies (80-160 mg) were extracted from the superficial portion of the vastus lateralis muscle with use of the percutaneous needle biopsy technique. The muscle samples were removed from the needle, oriented in tragacanth gum, immediately frozen in isopentane cooled by liquid nitrogen to  $-159^{\circ}$ C, and stored at  $-70^{\circ}$ C. Biopsies were taken at the beginning of the study (*week 1*) and every 2 wk during the 8-wk high-intensity training (weeks 3, 5, 7, and 9). Control subjects gave biopsies at these same time periods. Two training men and two training women missed one biopsy each (weeks 3 and 9). Therefore, a total of 161 biopsies were analyzed in the present investigation. Because of possible variations in fiber type distribution from superficial to deep and proximal to distal (4), attempts were made to extract tissue from approximately the same location each time using the prebiopsy scar and depth markings on the needle. As such, successive incisions were made  $\sim 0.5$  cm from each other going from medial to lateral. To ensure adequate sample sizes, large biopsies were obtained using a double-chop method (31, 32) combined with suction (10).

Light microscopy. The frozen biopsy samples were thawed to  $-20^{\circ}$ C and were serially sectioned ( $12 \,\mu$ m thick) for histochemical and histological analyses. Routine myofibrillar adenosine-triphosphatase (mATPase) histochemical analysis was performed using preincubation pH values of 4.3, 4.6, and 10.4 (5) to determine the muscle fiber type composition. Six fiber types (I, Ic, IIac, IIa, IIab, and IIb) were distinguished based on their staining intensities (28, 30) (Fig. 1). To evaluate the possible occurrence of subtle fiber type conversions, cross sections of the prebiopsy and all four postbiopsies from the same individual were placed on one glass cover slip and were assayed simultaneously for mATPase activity.

A composite photomontage of each mATPase preparation after preincubation at pH 4.6 was made using Polaroid micrographs ( $\times$ 56 magnification). These were used in combination with the other histochemical preparations to determine fiber type percentages and total fiber number in each biopsy. The cross-sectional areas of at least 50 fibers per major type (types I, IIa, and IIb) per biopsy were determined with use of direct tracings ( $\times 200$  magnification) and a digitizing tablet. Type IIab fibers were measured and added to the IIb group if <50 type IIb fibers were present. Damage from the initial biopsy (insertion of the biopsy needle and extraction of muscle tissue) caused the appearance of a minor population of degenerating and regenerating fibers in some of the postbiopsy samples of both control and training individuals. Also, a few atrophic fibers were observed in two of the prebiopsies (Fig. 1). A thorough assessment of this damage has been previously published (33). These fibers were excluded from measurement in the present study.

Myosin heavy chain (MHC) analysis. MHC analysis was performed on the biopsy samples using sodium dodecyl sulfate (SDS)-polyacrylamide electrophoretic techniques. The protocol for analyzing the specimens was based on the procedures of Perrie and Bumford (25) with modifications recently used for single human muscle fibers (28, 30). Briefly, four to six serial cross sections (20 µm thick) from each biopsy were placed into 0.5-1.0 ml of a lysing buffer containing 10% (wt/vol) glycerol, 5% (vol/vol) 2-mercaptoethanol, and 2.3% (wt/vol) SDS in 62.5 mM tris(hydroxymethyl)aminomethane · HCl buffer (pH 6.8) and were heated for 10 min at 60°C. Small amounts of the extracts  $(3-5 \mu l)$  were loaded on 4-8% gradient SDS-polyacrylamide gels with 3% stacking gels (3), run overnight (19-21 h) at 120 V, and stained with Coomassie Blue. MHC isoforms were identified according to their apparent molecular masses compared with those of marker proteins and migration patterns from single fiber analysis.

Statistical analyses. The statistical package for the biomedical sciences (BMDP) was used for the fiber type percentage data, and statistical software packages (Statgraphics and SPSSPC<sup>+</sup>) were used for all other statistical analyses. A repeated-measures two-way analysis of variance was used to detect possible changes occurring over time for muscle fiber cross-sectional area, absolute and relative maximal dynamic strength, and anthropometric data. A multivariate analysis was used to analyze the muscle fiber type percentage data. Regression analysis was used to fill in values for the four missing biopsies and to determine cross-sectional areas in biopsies with large group atrophy (7 of the 161 samples had large areas of damaged fibers from the previous biopsies). For the regression analysis, only one time period was missing. Therefore, four time periods were used to estimate the missing value. After a significant interaction between main effects, significant differences between the means were determined using a modified Tukey's post hoc test. A multivariate analysis of variance with repeated measures was used to analyze the hormone data with subsequent post hoc analysis performed when appropriate. Regression analysis was performed to examine the relationships between the changes in muscle fiber characteristics and hormonal concentrations with training. A systematic analysis was done, and only the significant values are reported (all other values were nonsignificant). Differences were considered significant at  $P \leq 0.05$ .

## RESULTS

Anthropometric measurements. No significant changes occurred over time in either group (training or control) for any of the anthropometric measurements (total body mass, fat-free mass, estimated percent body fat, or girth measurements) (Table 1).

Maximal dynamic strength. In men, maximal dynamic strength (relative to fat-free mass) for all three lower



FIG. 1. Serial cross sections of muscle samples taken from male control subject at beginning (A-C) and end (D-F) of study and from male strength-trained subject at beginning (G-I) and after 8 wk of high-intensity training (J-L). Sections were assayed for myofibrillar ATPase activity after preincubation at pH values of 10.2 (top row), 4.3 (middle row), and 4.6 (bottom row). Arrows, scattered atrophic fibers; I, type I; IC, type Ic; C, type IIac; A, type IIa; AB, type IIab; B, type IIb. Bar, 100  $\mu$ m.

limb exercises significantly increased after 4 wk of training (week 5) compared with initial values (Fig. 2). Likewise, in women, relative maximal dynamic strength increased after 4 wk for the leg extension and squat; however, relative maximal dynamic strength increased after just 2 wk for the leg press (Fig. 2). For both sexes, relative strength continued to significantly increase throughout the study such that the mean values were greater during week 7 than during weeks 1 and 3 and the mean values were greater during week 9 than during weeks 1, 3, 5, and 7 (Fig. 2). With very few exceptions, the mean absolute values gave similiar results.

The greatest absolute increases in all three exercises for both the men and women occurred after the initial 2 wk of training (week 3) and after the final 2 wk (week 9). Although the 1-RM absolute values for the women obtained at each time point for each exercise were significantly less than the corresponding 1-RM values obtained for the men, the relative values for all exercises for men compared with for women were similar throughout the study. Compared with the men's values, the training women's relative dynamic strength values for the squat, leg press, and leg extension were, respectively, 68, 77, and 67% at the beginning of the study and 88, 107, and 89% at the conclusion of the study (week 9) (Fig. 2). Both the men and women responded similarly over time to the squat and leg extension. However, there was a significant interaction over time for the leg press, indicating that the

Week	TBM, kg	FFM, kg	%BF		
	Trained	men (n = 13)			
1	$82.6 \pm 17.5$	69.1±10.4	$15.5 \pm 4.5$		
3*	$82.8 \pm 17.5$	$68.7 \pm 9.1$	$16.1 \pm 4.9$		
5	$82.3 \pm 17.0$	$70.0 \pm 10.3$	$14.6 \pm 4.7$		
7	$83.0 \pm 17.4$	$70.6 \pm 11.3$	$13.8 \pm 4.0$		
9*	$83.3 \pm 17.3$	$70.9 \pm 10.4$	$13.4 \pm 4.5$		
	Trained u	vomen (n = 8)			
1	$60.4 \pm 5.8$	$45.5 \pm 3.0$	$23.8 \pm 5.1$		
3†	$61.0 \pm 6.1$	$45.5 \pm 2.7$	$24.6 \pm 4.6$		
5	$61.1 \pm 5.7$	$47.0 \pm 2.7$	$22.1 \pm 4.5$		
7	$61.1 \pm 5.4$	$47.4 \pm 1.9$	$21.3 \pm 4.9$		
<b>9</b> †	$61.7 \pm 5.3$	$47.9 \pm 1.8$	$20.9 \pm 4.8$		
	Control	men (n = 7)			
1	$76.9 \pm 13.8$	$66.8 \pm 9.7$	$12.5 \pm 4.4$		
3	$76.7 \pm 13.8$	$66.0 \pm 9.5$	$13.6 \pm 4.2$		
5	$76.9 \pm 13.3$	$67.0 \pm 9.5$	$13.1 \pm 3.9$		
7	$77.0 \pm 14.0$	$66.8 \pm 9.5$	$13.2 \pm 4.1$		
9	$77.0 \pm 13.8$	$66.6 \pm 9.6$	$13.2 \pm 4.0$		
	Control u	oomen (n = 5)			
1	$68.8 \pm 12.8$	48.7±7.0	$28.3 \pm 3.1$		
3	$67.1 \pm 13.2$	$46.6 \pm 6.4$	$29.5 \pm 5.3$		
5	$68.1 \pm 14.0$	$48.6 \pm 8.1$	$28.2 \pm 4.5$		
7	$68.6 \pm 14.2$	$48.7 \pm 7.0$	$28.6 \pm 4.7$		
9	$68.3 \pm 14.3$	$46.9 \pm 5.5$	$29.5 \pm 4.7$		

TABLE 1. Anthropometric measurements fromresistance-trained and control men and women

Values are means  $\pm$  SD; *n*, no. of subjects except \**n* = 12 and †*n* = 7. TBM, total body mass; FFM, fat-free mass; %BF, estimated percent body fat. Week 1 is preexercise value.

men and women did not perform the same for this exercise (Fig. 2).

Cross-sectional area measurements. Although there were apparent gradual increases in the cross-sectional areas of all three major fiber types from the training individuals, no significant differences were found across time for any fiber type (Fig. 3). Also, no significant differences in cross-sectional area were found over time for any of the fiber types from the control men or women (Fig. 3).

Fiber type analysis. A significant decrease in the percentage of histochemically assessed type IIb fibers occurred across time for both the training men and training women. This decrease became significant after just 2 wk of high-intensity training for the women and after 4 wk for the men (Table 2) and corresponded to an observed decrease in MHC IIb (Fig. 4). Although a trend existed for a concomitant increase in the percentage of histochemically assessed type IIa fibers, these values were nonsignificant. In addition, there was a significant increase in the percentage of type I fibers after 4 wk of training for the women (Table 2). However, this increase was transient and subsequently decreased to nonsignificant levels after both 6 and 8 wk of training. No significant changes in fiber type composition or MHC content were found in the control muscles (Table 2) (Fig. 4).

Resting hormone concentrations. Resistance training caused a significant increase in the resting serum testosterone concentrations in the men (Fig. 5). These testosterone levels remained elevated for the duration of the study and were significantly greater than the corresponding control values at the same time periods (Fig. 5). In addition, significant correlations were found for the training men between the percentage of type IIa fibers and serum testosterone levels ( $r^2 = 0.39$ ) and also between the percentage of type IIb fibers and serum testosterone levels ( $r^2 = 0.46$ ). As expected, testosterone concentrations were dramatically higher at all time points in



FIG. 2. Relative maximal dynamic strength [1-repetition maximum/fat-free mass (1 RM/FFM)] of training men and women for leg press (A), leg extension (B), and squat (C). Values are means  $\pm$  SE. Significantly different from: \* week 1; † weeks 1 and 3; × weeks 1, 3, and 5;  $\star$  weeks 1, 3, 5, and 7.



FIG. 3. Bar graphs of mean cross-sectional areas of fiber types I, IIa, and IIb from trained (solid bars) and control (hatched bars) men (A) and women (B).

men than in women. No significant changes in resting serum testosterone concentrations were observed over the 9 wk in the control groups or in the training women.

Serum cortisol levels were significantly lower in the training men at weeks 7 and 9 than at week 1 (preexercise) (Fig. 5). In addition, a significant inverse correlation  $(r^2 = 0.47)$  was found between the changes in the cross-sectional area of the type IIb fibers (increased) and the resting serum cortisol concentrations (decreased) in the training men. No significant changes in serum cortisol

concentration were observed in the women (control or training) or in the men's control group. In addition, serum cortisol values were significantly lower in the training men than in either the training or control women at weeks 7 and 9 (Fig. 5). Although the resting growth hormone concentrations for the women were significantly higher than for the men at all time points, no significant changes or differences were found in serum growth hormone levels for either the men or women over the 9-wk period (Fig. 5).

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TABLE 4	2.	muscie	noer	<i>iype</i>	percentages	$\iota \iota \iota$	resistance-	iruineu	unu	control	men	unu	women

Week	Type I	Type Ic	Type IIac	Type IIa	Type IIab	Type IIb	N
			Train	ed men (n = 13)			
1	$40.7 \pm 7.9$	$0.4 \pm 0.3$	$0.5 \pm 0.6$	31.1±9.1	$6.6 \pm 3.0$	20.7±8.4	$1,156 \pm 408$
3*	42.4+11.8	$0.6 \pm 0.7$	$2.1 \pm 2.1$	$34.9 \pm 7.4$	$5.7 \pm 4.8$	$14.3 \pm 10.2$	$1,331\pm345$
5	44.7+15.4	0.5+0.6	$2.6 \pm 2.4$	$34.9 \pm 10.4$	$5.9 \pm 4.3$	11.4±9.9‡	$1,092 \pm 347$
7	41 7+8 2	1.8+3.3	2.7+2.6	$40.0 \pm 7.8$	$6.8 \pm 4.3$	$7.0 \pm 7.7 \pm$	1,119±282
9 <b>*</b>	40.0±9.0	2.1±4.9	$2.0 \pm 1.8$	37.9±9.0	$8.5 \pm 4.4$	9.5±8.9‡	$1,134\pm295$
			Traine	ed women (n = 8)			
1	38.8±8.8	0.3±0.6	$0.8 \pm 1.5$	$31.8 \pm 5.4$	$6.9 \pm 5.7$	$21.4 \pm 8.1$	$1,303\pm527$
- 3†	$47.0 \pm 10.1$	$0.6 \pm 1.1$	$1.0 \pm 1.6$	$32.0 \pm 3.9$	$6.8 \pm 4.1$	$12.6 \pm 10.8 \ddagger$	1,640±794
5	47.6+9.5t	$0.6 \pm 1.0$	$1.5 \pm 1.8$	$33.1 \pm 13.0$	$5.5 \pm 2.3$	11.7±8.6‡	$1,663\pm583$
7	43.7+9.1	$1.0 \pm 1.2$	$1.6 \pm 1.6$	$39.8 \pm 7.6$	$7.1 \pm 5.2$	6.8±6.0‡	1,526±626
9†	44.3±7.6	$0.8 \pm 1.1$	$1.4 \pm 1.6$	$38.8 \pm 12.8$	$6.8 \pm 4.0$	7.9±6.8‡	$1,827 \pm 467$
			Cont	rol men (n = 7)			
1	44.9±10.4	0.1±0.2	$1.7 \pm 1.7$	$33.3 \pm 12.3$	$3.3 \pm 1.1$	16.7±7.9	$1,355 \pm 599$
3	$51.0 \pm 8.4$	$0.2 \pm 0.2$	$1.4 \pm 1.2$	$32.7 \pm 4.9$	$3.0 \pm 0.6$	$11.7 \pm 3.6$	1,174±454
5	47.1±9.2	$0.3 \pm 0.4$	$1.7 \pm 1.8$	$33.1 \pm 10.8$	$3.1 \pm 0.8$	$14.7 \pm 7.2$	1,145±560
7	47.2+11.7	$0.2 \pm 0.2$	$3.7 \pm 7.6$	32.4±9.7	$3.1 \pm 1.1$	$13.4 \pm 6.3$	$1,289 \pm 283$
9	47.7±13.8	$1.3 \pm 1.4$	$1.6 \pm 1.9$	$32.0 \pm 9.0$	$3.1 \pm 2.1$	$14.3 \pm 6.7$	1,502±431
			Contro	ol women (n = 5)			
1	39.1±5.3	1.1±1.0	$0.2 \pm 0.2$	25.4±8.0	4.5±1.7	29.7±7.3	1,419±432
3	49.8±10.7	$0.3 \pm 0.3$	$0.1 \pm 0.1$	$20.6 \pm 6.6$	$4.8 \pm 2.3$	24.4±9.9	$1,189 \pm 267$
5	44.4±8.8	$0.3 \pm 0.4$	0.4±0.3	$24.6 \pm 9.4$	$3.6 \pm 1.4$	$26.7 \pm 13.9$	$1,126 \pm 462$
7	$41.5 \pm 6.3$	0.7±0.7	$1.3 \pm 1.0$	$25.4 \pm 6.2$	$3.8 \pm 2.6$	$27.3 \pm 1.3$	$1,954 \pm 253$
9	41.2±7.9	$2.1 \pm 2.4$	$2.3 \pm 3.9$	$18.3 \pm 3.2$	4.1±2.2	$32.0 \pm 9.0$	1,348±598

Values are means  $\pm$  SD in % for fiber type and means  $\pm$  SD for no. for fibers analyzed per biopsy (N); n = no. of subjects except \* n = 12 and  $\dagger n = 7$ .  $\ddagger$  Significantly different (P < 0.05) from week 1 (preexercise) values.



FIG. 4. Myosin heavy chain (MHC) analysis from biopsies obtained from female training (T) and control (C) subjects. Although MHC content is somewhat variable from biopsy to biopsy, note gradual loss of MHC IIb over time for training women.

#### DISCUSSION

Previous work from our laboratory has indicated that significant hypertrophy of all three major fiber types (increases of 15, 45, and 57% for types I, IIa, and IIb, respectively) can be induced in the vastus lateralis muscle of women after long-term (20 wk) high-intensity resistance training (31). The possibility of women making such dramatic increases in muscle fiber size is not entirely surprising on the basis of empirical observations and investigations demonstrating increases in whole muscle crosssectional area of resistance-trained women (8, 26). Recently, a hypertrophic response has also been demonstrated in the vastus lateralis muscle of elderly women subjected to 12 wk of resistance training (20% increase in cross-sectional area of fast type II fibers) (6). Interestingly, apparent fast fiber type conversions (type IIb  $\rightarrow$ IIa) have also been reported after long-term resistance training (31). Indeed, very few type IIb fibers were found after 20 wk of high-intensity training (16.2% pretraining vs. 2.7% posttraining). Such conversions had previously been reported only for normal human muscle as a result of endurance training (see Ref. 29).

A follow-up study was performed to verify these muscular adaptations in resistance-trained women and to investigate the effects of a much shorter duration training period (32). After 6 wk of high-intensity resistance training in a group of nonpreviously strength-trained women, again the cross-sectional areas of all three major fiber types significantly increased (type I 15.6%, type IIa 17.3%, and types IIab + IIb 28.1%) and a significant decrease in the percentage of type IIb fibers occurred (24.9% pretraining vs. 6.7% posttraining) (32). Similar changes in fiber type distribution have recently been reported in the vastus lateralis muscle of men after 19 wk of resistance training (1, 13).

To the authors' knowledge, no previous resistance training study has attempted to establish the time course for muscular adaptations with use of successive biopsies. As such, the current investigation has revealed information that supports and extends these observations from previous studies. It is clear that while skeletal muscle is undergoing neural adjustments in response to high-intensity strength training concomitant intramuscular adaptations are also taking place.

Indeed, it has been shown that a single bout of heavyresistance exercise can increase muscle protein synthesis for up to 24 h postexercise (7). Such increases in protein synthesis undoubtedly contribute to an increase in the amount of contractile proteins, which ultimately leads to a significant increase in cross-sectional area (12). Although nonsignificant over time, there was a trend in the present investigation toward a gradual increase in the areas of all three fiber types that, after 8 wk of resistance training, showed similar percent increases to those previously found after 6 wk of training (32). Obviously, the addition of thick and thin filaments is a gradual process.

Although significant changes in the cross-sectional area appear to take at least 6–8 wk, the replacement of MHC IIb by MHC IIa occurs earlier. In the present study, significant changes in the percentage of type IIb fibers were detected after just 2 wk of workouts (5 total workouts: 4 high-intensity workouts and 1 testing session) for the women. This alteration in fiber type composition was further supported by MHC analysis. It is not known to what extent this remodeling within the muscle fibers may contribute to increases in maximal dynamic strength. However, gradual increases in the number and/ or size of the myofibrils, and perhaps the fast fiber type conversions of type IIa  $\rightarrow$  IIb, should contribute to strength gains.

The anthropometric and muscular adaptations occurring throughout the 8-wk strength training for the lower extremity were similar for the men and women and indicate a qualitative similarity between these two groups that has been observed in other studies (see Ref. 23). Although gender differences do exist (compared with men, women generally have significantly less total and lean body mass, greater percent body fat, significantly smaller cross-sectional area of all three major fiber types in the vastus lateralis muscle, and a different hierarchy of fiber type sizes), these differences did not contribute to any apparent adaptive differences in the early phase of heavy-resistance training. However, hormonal mechanisms, which may play a role in strength adaptations by



FIG. 5. Means  $\pm$  SD of resting hormone concentrations (testosterone, cortisol, and growth hormone) for men (A) and women (B). •, Trained subjects; •, control subjects. \* Significantly different ( $P \le 0.05$ ) from corresponding week 1 (preexercise) values.

stimulating muscle growth, do appear to differ between men and women.

Animal studies have demonstrated that testosterone

and glucocorticoid levels relate to changes in skeletal muscle fiber types and alterations in isomyosins in cardiac muscle (18, 19). Data from the present study suggest

that these specific hormonal mechanisms may also be operational during the early phase of heavy-resistance training in previously untrained men. Increases in resting levels of testosterone and reductions in cortisol concentrations should create an enhanced environment for growth, which would be conducive to alterations in amino acid uptake and protein synthesis for the working muscles (11). On the other hand, the observation of no changes in testosterone and cortisol concentrations in the training women suggests gender-specific differences in the hormonal responses of women to heavy-resistance exercise (20, 21, 35). For growth hormone, the higher concentrations and the greater interindividual variations in women than in men have been previously reported and may be due to menstrual status (21). The lack of any association of growth hormone to muscle fiber changes may indicate a need for more frequent measurements during the day and, perhaps, measurement of insulinlike growth factor I (which is stimulated by growth hormone and is a potent anabolic factor) (27).

In conclusion, analyses of biopsies taken every 2 wk during an 8-wk heavy-resistance training regimen have given further insight into the dynamic nature of skeletal muscle. If sufficiently stressed, the muscle need not be active for extremely long periods to cause an alteration in fiber type composition (type IIb  $\rightarrow$  IIa). The time course for the alteration of the phenotypic expression of specific contractile proteins appears to be an adjustment that can occur after only a few workouts. In contrast to these fast fiber type conversions is a much more gradual hypertrophic response. According to the parameters measured in the current investigation, skeletal muscle from men and women appears to respond in a similar manner to the heavy-resistance training. However, one gender difference may be reflected in possible hormonal mechanisms that may stimulate muscle growth: for the men, increased testosterone and decreased cortisol levels favor an environment for increased protein synthesis. It is clear that, although neural adaptations play an important role in the early phase of resistance training, during this time significant changes contributing to strength gains are also taking place within the muscle.

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Portions of this work have been presented in abstract form (17).

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